Symposium

The Nature and Application of Biocontrol Microbes III: *Pseudomonas* spp.

Pseudomonas Biocontrol Agents of Soilborne Pathogens: Looking Back Over 30 Years

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ABSTRACT

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Pseudomonas spp. are ubiquitous bacteria in agricultural soils and have many traits that make them well suited as biocontrol agents of soilborne pathogens. Tremendous progress has been made in characterizing the process of root colonization by pseudomonads, the biotic and abiotic factors affecting colonization, bacterial traits and genes contributing to rhizosphere competence, and the mechanisms of pathogen suppression. This review looks back over the last 30 years of *Pseudomonas* biocontrol research and highlights key studies, strains, and findings that have had significant impact on shaping our current understanding of biological control by bacteria and the direction of future research.

Pseudomonas spp. are aerobic, gram-negative bacteria, ubiquitous in agricultural soils, and are well adapted to growing in the rhizosphere. Pseudomonads possess many traits that make them well suited as biocontrol and growth-promoting agents (135). These include the ability to (i) grow rapidly in vitro and to be mass produced; (ii) rapidly utilize seed and root exudates; (iii) colonize and multiply in the rhizosphere and spermosphere environments and in the interior of the plant; (iv) produce a wide spectrum of bioactive metabolites (i.e., antibiotics, siderophores, volatiles, and growth-promoting substances); (v) compete aggressively with other microorganisms; and (vi) adapt to environmental stresses. In addition, pseudomonads are responsible for the natural suppressiveness of some soils to soilborne pathogens (137). The major weakness of pseudomonads as biocontrol agents is their inability to produce resting spores (as do many *Bacillus* spp.), which complicates formulation of the bacteria for commercial use. The purpose of this review is to look back over the last 30 years of *Pseudomonas* biocontrol research and identify some key studies and findings that have helped to shape our current understanding of the biocontrol activity of these bacteria and the direction of future research.

CLASSIC STRAINS AND NOVEL CONCEPTS

Berkeley strains. One lineage of contemporary *Pseudomonas* biocontrol research can be traced to bacterization studies with fluorescent pseudomonads beginning in the 1970s at the University of California, Berkeley. Bacterization is the process of inoculating plant seeds, seed pieces, or roots with bacteria to enhance plant growth (54). These studies demonstrated that certain fluorescent *Pseudomonas* spp. improved the growth of potato sugar beet and radish when applied to seeds or seed pieces (108,109). Examples of strains that have provided enhanced growth include TL-3 (13), B10, A1, and E6 (58), isolated from potato tubers and roots, and SH-5, isolated from sugar beet roots (116). All of these strains were classified as *P. fluorescens-putida* types. For example, in 11 trials conducted at multiple field sites over 3 years, bacterization of potato seed pieces with TL-3 resulted in an average yield increase of 10% compared with the noninoculated control. These results were statistically significant at 6 of 11 sites (13,58). In five of nine field trials, SH-5 significantly increased the yield of sugar beet an average of 12%. Growth promotion following bacterization also was demonstrated for radish (56) and ornamental plants (145). Growth promotion in these studies apparently resulted from suppression of "minor pathogens." These studies, and many others, resulted in the following new terms, findings, and concepts.

- Rhizobacteria: plant-associated bacteria that are able to colonize and persist on roots (54).
- Plant growth-promoting rhizobacteria (PGPR): rhizobacteria that have the ability to promote the growth of plants following inoculation onto seeds or subterranean plant parts (54). Initial studies of PGPR focused primarily on fluorescent pseudomonads, but it is now known that PGPR include a diverse assemblage of bacteria representing a broad spectrum of genera.
- PGPR strains are aggressive colonists of the rhizosphere environment and they can persist for the duration of the growing season (5,58).
- PGPR can preempt the establishment of other rhizosphere microorganisms through competition for favored sites on the root and in the rhizosphere (57,116).
- Production of siderophores (e.g., pyoverdine and pseudobactin) by PGPR, which can limit the amount of iron available to pathogens for growth, was identified as a new mechanism of biological control (53). Strain B10 was used as a model organism in studies of siderophore production and the role of siderophores in biological control (58).

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- Pseudomonads improve plant growth by suppressing either "major" (produce well-known root or vascular diseases with obvious symptoms) or "minor" (parasites or saprophytes that damage mainly juvenile tissue such as root hairs and tips and cortical cells) pathogens (103).

Dutch strains. A second lineage of contemporary *Pseudomonas* biocontrol research can be traced to bacterizaton studies with fluorescent pseudomonads initiated at the Phytopathologisch Laboratorium, "Willie Commelin Scholten" (WCS), Baarn, The Netherlands. Dutch researchers observed that as the frequency of potato production in a field increased, the yields decreased. Potatoes grown every third year (short potato rotation) or continuously in a field yielded 10 to 15% and 30% less, respectively, than potatoes grown in a field every sixth year (long potato rotation) (41,103,104). They showed that bacterization of seed tubers with pseudomonads such as *P. fluorescens* strains WCS374 and WCS365 and *P. putida* strain WCS358 resulted in an increase in yield in short- but not long-rotation soils (7,33–35). Deleterious rhizosphere microorganisms (DRMO), particularly hydrogen cyanide (HCN)-producing pseudomonads, were thought to be the targets of the PGPR. DRMO increased to population densities sufficient to cause damage in the short but not the long rotations, thus accounting for the influence of crop rotation on PGPR activity (103). Other major pathogens probably also contributed to the poor growth of potatoes in short rotations. Siderophore production and induced resistance were identified as the primary mechanisms of pathogen suppression by the Dutch pseudomonads (7,8,97). WCS strains (i.e., WCS374, WCS365, WCS417, and WCS358) are especially notable because they have been used extensively during the past 25 years as model organisms in studies of siderophore production and uptake, bacterial traits and genes involved in root colonization, and induced systemic resistance (ISR) (25–27,81,124,125).

Antibiotic producers. A third lineage of contemporary *Pseudomonas* biocontrol research can be traced to bacterization studies conducted at several laboratories with fluorescent pseudomonads that produce antibiotics such as phenazine-1-carboxylic acid (PCA) and other derivatives, 2,4-diacetylphloroglucinol (DAPG), pyrrolnitrin (Prn), and/or pyoluteorin (Plt). Biocontrol agents produce a wide variety of antibiotics; however, the lack of definitive experimental evidence for the role of antibiotics in the biocontrol process led to an ongoing debate over most of the last century (30,141). However, this changed, beginning in 1988, with definitive studies showing an important role for antibiotics in biocontrol mediated by pseudomonads (119).

P. fluorescens strain 2-79 and *P. chlororaphis* 30-84 (formerly *P. aureofaciens*) were isolated from wheat grown in take-all suppressive soils from fields near Lind, Washington (136) and Glen Elder, Kansas (96), respectively. Bacterization of spring or winter wheat seeds with either of these two strains resulted in significant suppression of take-all in about 60% of field trails. For example, strain 2-79 increased yields an average of 17% in experimental plots and 11% in commercial scale tests (135). Both strains produce PCA and a pyoverdine siderophore (144). In addition, 2-79 produces anthranilic acid; and 30-84 produces two other phenazines, 2-hydroxyphenazine-1-carboxylic acid (2-OH-PCA) and 2-hydroxyphenazine (2-OH-PZ) as well as HCN (96).

P. fluorescens strains CHA0, Pf-5, Q2-87, and F113 have been used as model strains in studies of the biosynthesis of DAPG, Prn, and Plt, and in studies of the role of these antibiotics in pathogen suppression. *P. fluorescens* strain CHA0 was isolated from roots of tobacco grown near Payern, Switzerland, in a soil naturally suppressive to black root rot of tobacco caused by *Thielaviopsis basicola* (115). CHA0 produces DAPG, Plt, Prn, HCN, indoleacetic acid, salicylic acid, pyochelin, a pyoverdine siderophore (pseudobactin), and other bioactive metabolites (129). Thus, this strain has one of the broadest repertoire of potential biocontrol and growth-promoting mechanisms of any PGPR described so far. CHA0 suppresses root rots of tobacco and tomato, Pythium damping-off of cucumber, and take-all of wheat (28,52,106). The contribution of each metabolite to disease suppression is dependent upon the host crop and target pathogen. For example, production of DAPG was the primary mechanism of suppression of take-all of wheat by CHA0, whereas both DAPG and HCN contributed to suppression of black root rot of tobacco (37,52,130). Plt was involved in suppression of damping-off of cress and cucumber by this bacterium (77). Here it is interesting to note that HCN production by pseudomonads provides a beneficial effect in terms of biocontrol activity. Thus, HCN is an example of a metabolite that can differentially affect plant growth depending on the producer strain, the amount of HCN accumulating in microsites in the rhizosphere, and the crop species grown.

P. fluorescens Pf-5 was isolated from the rhizosphere of cotton and is quite similar to CHA0 in that it produces DAPG, Plt, and Prn (46,47,86). Strain Pf-5 suppressed damping-off of cotton caused by *Pythium ultimum* or *Rhizoctonia solani*. Purified Prn and Plt obtained from Pf-5 provided the same protection against Rhizoctonia and Pythium damping-off, respectively, as did the bacterium. *P. fluorescens* Q2-87 was isolated from wheat roots grown in a suppressive soil from a field near Quincy, Washington. Q2-87 produces DAPG and HCN, but only DAPG contributed to its biocontrol activity against take-all (39,128). In field studies, take-all suppression by Q2-87 was greatest when it was used in combination with three other strains also isolated from the Quincy suppressive soil (92). *P. fluorescens* F113 was isolated from sugar beet in Ireland and suppressed damping-off of sugar beet caused by *Pythium ultimum* and cyst nematode and soft rot of potato (18, 19,29,111). These studies, and many others, resulted in the following novel findings and concepts.

- The research with Pf-5 by Howell and Stipanovic (46,47) sparked interest in the role of antibiotic production in *Pseudomonas* biocontrol activity.
- Studies of the suppression of take-all by *P. fluorescens* 2-79 provided the first unequivocal evidence that production of an antibiotic in situ contributed to biocontrol activity (119). This work outlined a genetic strategy known as "Molecular Koch's Postulates" that is still commonly used to determine the role of a specific metabolite in the biocontrol process: (i) mutagenesis of a biocontrol agent (e.g., transposon mutagenesis), (ii) screening for loss of the trait, (iii) genetic complementation of mutants to restore the target trait, and (iv) comparison of the biocontrol abilities of the parental strain, mutant, and complemented mutant (138).
- Studies with the phenazine producers 2-79 and 30-84 demonstrated that antibiotics can be readily isolated from the rhizosphere environment (120), providing further evidence of the importance of antibiosis in biological control. It is now common to isolate and quantify antibiotic production in the rhizosphere and spermosphere (118).
- Phenazines, DAPG, Prn, and Plt are four of the most common antibiotics produced by *Pseudomonas* biocontrol agents. *Pseudomonas* spp. that produce these antibiotics became a major focus of biocontrol research, and many genes involved in the regulation and synthesis of these compounds are now known (1,4,9,17,23,29,32,38,40,51,60,62,76,78, 85,87,91,94,95,101,106). Strains CHA0, Pf-5, 30-84, and F113 have been especially valuable in the identification and characterization of regulatory genes of metabolite production: (i) *gacS*/*gacA*—a two-component sensor-regulator pair controlling extracellular metabolites and exoenzymes (62, 140); (ii) *rsmZ*, *rsmY*, and *rsmX*—small untranslated regulatory RNAs (51) that modulate activity of translational repressors RsmA and RsmE (99,122,123); (iii) *rpoS* and *rpoN*—alternative sigma factors (101); (iv) *phzI* and *phzR*—pathway-specific regulators of phenazine biosynthesis and quorum sensing (95); (v) *phlF*—repressor of DAPG syn-

thesis (9); and (vi) *pltR*—repressor of pyoluteorin production (85).
- The complete genome of the biocontrol agent *P. fluorescens* Pf-5 has been determined (90).

ISR pseudomonads. A fourth lineage of contemporary *Pseudomonas* biocontrol research can be traced to independent demonstrations in 1991 by research groups in The Netherlands, the United States, and Sweden that some pseudomonads colonizing the roots protected plants from various pathogens by inducing systemic resistance. For example, van Peer et al. (126) reported that *Pseudomonas* strain WCS417 induced resistance in carnation against Fusarium wilt caused by *Fusarium oxysporum* f. sp. *dianthi* when the roots were inoculated with bacteria 1 week prior to stem inoculation with the pathogen. This strain was isolated from the wheat rhizosphere and also promoted the growth of several crops. Subsequently, strains WCS417 and WCS374 were shown to induce resistance in radish against *F. oxysporum* f. sp. *raphani* and other pathogens (42). The O-antigenic side chain of the lipopolysaccharide, present on the outer membrane of strains WCS374 and WCS417, appeared to be the determinant responsible for the induction of resistance in radish (63). Strain WCS374 applied as a seed treatment to radish seeds provided an average reduction in Fusarium wilt of 42% and an average yield increase of 45%. Radish seeds coated with this strain, trade name BioCoat, were sold for a short time (63). Wei et al. (131) demonstrated that *P. putida* 89B-27 and other nonpseudomonads induced resistance in cucumber leaves to anthracnose, caused by *Colletotrichum orbiculare*. Strain 89B-27 also induced resistance in cucumber against angular leaf spot, caused by *P. syringae* pv. *lachrymans* (65), and Fusarium wilt, caused by *F. oxysporum* f. sp. *cucumerinum*. This strain also induced resistance against cucumber pathogens in the field (132). Alström (2) reported ISR in bean against halo blight caused by *P. syringae* pv. *phaseolicola* by seed bacterization with *P. fluorescens* strain S97. Here, there was a correlation between reduction in symptom expression and lower population density of *P. syringae* pv. *phaseolicola* in the leaves (3). These studies are highly significant because they identified an entirely new mechanism of biological control by pseudomonads and other PGPR; ISR is now intensively studied worldwide.

ROOT COLONIZATION AND NOVEL CONCEPTS

The dynamics of colonization. The high microbial diversity, density, metabolic activity, and competition occurring in the rhizosphere environment represents a formidable "biological buffering" (137) that generally limits the establishment of introduced, foreign microorganisms into the rhizosphere. Thus, one must marvel at the ability of introduced pseudomonads and other PGPR to colonize roots and provide protection against major and minor soilborne pathogens. Several definitions of root colonization by rhizobacteria were proposed (54,55,88,109) and most included components of movement of the rhizobacteria from an inoculum source to the roots, multiplication, and persistence, all in the presence of native soil microflora. Weller and Thomashow (139) defined root colonization as the process whereby rhizobacteria introduced on seeds, vegetatively propagated plant parts, or into the soil become distributed along roots growing in raw soil, multiply, and then survive for several weeks in the presence of indigenous soil microflora. Root colonization included colonization of the rhizosphere, rhizoplane, and/or inside the root. Rhizosphere competence describes the relative root-colonizing ability of a rhizobacterium (135).

During the last 30 years, experimental systems using pseudomonads have made significant contributions to our understanding of the process of root colonization, the biotic and abiotic factors affecting colonization, and the bacterial genes and traits that contribute to rhizosphere competence. Root colonization has remained a focus of much research because of the positive relationship between colonization and pathogen suppression in many biocontrol systems. Arguably, the work of Bahme and Schroth (5) was the "gold standard" of root colonization studies. In a pair of elegant experiments conducted at Tulelake, CA (Osborn silty clay-loam) and at Bakersfield, CA (Hesperia sandy loam), they determined the spatial-temporal colonization pattern of seed piece-applied *P. fluorescens* strain A1-B at all stages of potato development and on all below-ground plant parts. The comprehensiveness and attention to details of this study were especially notable. For example, early in the growing season the authors could remove an entire root system with a spade but in order to insure that an entire root was removed later in the season, they dug trenches alongside the plants. Other notable colonization studies included the use of (i) *Pseudomonas* strains A1 and SH5 to describe the distribution of introduced pseudomonads on and among root systems (70); (ii) *P. fluorescens* PRA25 to describe the movement of rhizobacteria through soil and the effect of temperature on colonization (11,64); (iii) *P. fluorescens* 2-79 to describe the relationship between inoculum dose, colonization, and biocontrol activity, and the effect of matric potential on colonization (12,48,133); and (iv) *P. fluorescens* WCS365 to identify rhizosphere competence traits and genes (71). These studies, and many others, resulted in the following novel findings and concepts.

- Passive carriage on the root apex (48,110) and with percolating water (64,72,84,89,117,121) function in concert to move rhizobacteria from inoculum sources on seeds and planting material throughout the root system and into the bulk soil (long-distance transport). Active bacterial movement (10,24,102) plays a role in colonization on a much smaller scale.
- Rhizobacteria, when applied to seeds or planting material, can become widely distributed throughout a root system (5,133,134).
- Population sizes of introduced rhizobacteria are greatest on roots and in soil nearest the inoculum source and decline with increasing distance from the source of inoculum (5,134).
- Populations of introduced rhizobacteria on roots and other underground plant parts are not normally distributed (5,70).
- Root colonization by rhizobacteria varies among fields, soil types, and crops (5).
- The method of inoculum delivery affects spatial-temporal colonization patterns of rhizobacteria on roots and underground plant parts (6).
- Population densities of introduced rhizobacteria in the rhizosphere usually are greatest soon after planting and gradually decline throughout the growing season, often dropping below the detection limit (8,48,59,70,73,79,97).

Bacterial traits and genes contributing to rhizosphere competence. During the last 25 years, studies of rhizosphere competence traits and genes have focused extensively on pseudomonads and have resulted in three major conclusions. First, rhizosphere competence is governed by many genes and traits, and in a single strain, multiple traits may be involved in the process. This should not be surprising because root colonization is a multistage process. Secondly, the contribution of a given trait or gene to rhizosphere competence may be strain-specific. Finally, the relative importance of a trait or gene is affected by the plant species, soil type, environmental conditions, and the type of assay used to study the trait. The following are traits or genes that have been shown to contribute to rhizosphere competence in at least one rhizobacterium.

- Ability to compete for or produce limiting resources including the following: vitamins (biotin, thiamine) (114), amino acids (16,71,112,127), organic acids (71), sugar phosphates (67), and iron (43,45,69,82,83,98).
- Rapid growth rate (22,31,61,113).

- Cell surface structures and traits: lipopolysaccharide (22, 27,113), flagella/motility (16,22,26,71,113), chemotaxis (24), and NADH dehydrogenase (14,22).
- Ability to survive exposure to physical and chemical stresses: heat, desiccation, presence of reactive oxygen species, high osmolarity, low matric potential, and bacteriostatic levels of putrescine (36,49,50,61,68,74,101,107).
- Global regulators facilitating responses to environmental change: GacS and GacA (40,75,84,105), sigma factor (75,107,140), and quorum sensing (interpopulation and intrapopulation signaling) (15,66,93,142,143,146).
- Ability to create a phenotypically diverse population: phase variation/site-specific recombinase (16,20,21,44,100).
- Production of phenazine antibiotics (80).

FUTURE PROSPECTS AND DIRECTIONS

Tremendous progress has been made over the past 30 years in understanding the process of root colonization by pseudomonads and in characterizing the biotic and abiotic factors affecting colonization, the genes contributing to rhizosphere competence, and the diverse mechanisms by which pseudomonads suppress soilborne pathogens. This wealth of knowledge has provided a firm foundation for *Pseudomonas* research in the 21st century that must now be applied to advance broader incorporation of these bacteria into sustainable strategies for the management of soilborne pathogens. In the short term, the technology already exists to directly identify biocontrol agents active against target pathogens, to select strains with an affinity for particular crops or cultivars, to engineer strains for greater efficacy and reliability, and to develop and exploit soils naturally suppressive to particular pathogens. New insights are certain to be gained from the recently published genomic sequence of *P. fluorescens* Pf-5, which already has revealed biosynthetic potential for many previously undetected compounds likely to contribute to the broad antifungal activity of this strain (90). Perhaps the greatest remaining challenge facing *Pseudomonas* biocontrol research is the development of new formulations. Even here, progress has resulted from recognition of the impact of the production process on the quality of biocontrol products, and high-throughput methods have been developed to identify factors that affect efficacy and shelf life. In total, tremendous progress has made over the last 30 years, which bodes well for the future of biocontrol with *Pseudomonas* spp.

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